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## Cranes of the World: Sandhill Crane (*Grus canadensis*)

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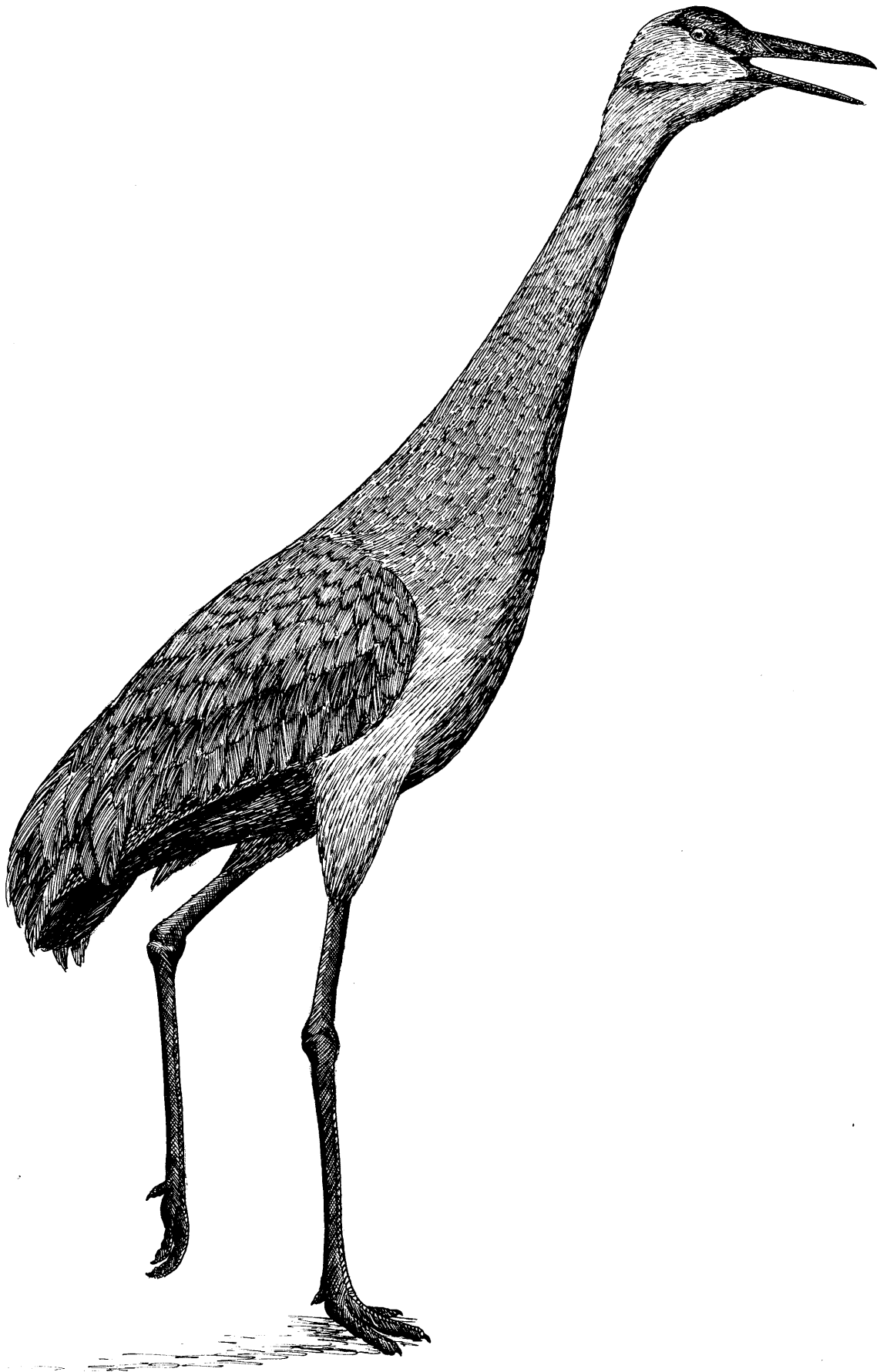
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# Sandhill Crane

## *Grus canadensis* (Linnaeus) 1758

**Other Vernacular Names.** Canadian crane, Little brown crane; Grue du Canada (French); Kanadischer Kranich (German); Kanada-zuru (Japanese); Kanadaski zhuravl (Russian); Grulla del Canada (Spanish).

**Range.** Breeds in extreme northeastern Siberia and in North America from Alaska to Baffin Island, south to northeastern Colorado, Minnesota, Wisconsin, and Michigan. Additional nonmigratory populations exist in Georgia, Florida, Mississippi, Cuba, and the Isle of Pines. The migratory races winter from California and Baja California eastward to New Mexico, Texas, and Florida. The breeding range was formerly much more extensive in the United States, extending south to Nebraska, Indiana, and Ohio.

**Subspecies.**

*G.c. canadensis*: Lesser sandhill crane. Breeds in northeastern Siberia along the lower Anadyr River and its tributaries, and recorded from the Chukotski Peninsula, Wrangel Island, and the arctic USSR coastline west to the Indigirka River. Breeds on St. Lawrence Island and in North America from northern Alaska to Baffin Island, probably south to Cook Inlet in Alaska, and to central or southern Mackenzie, southern Keewatin, and Southampton Island. Intergrades with *rowani* to the south, making range limits uncertain. Winters in central California, and from eastern New Mexico and northwestern Texas south to Chihuahua and rarely to central Mexico.

*G.c. rowani*: Canadian sandhill crane. Breeds in central Canada, probably from eastern British Columbia through the northern portions of Alberta, Saskatchewan, and Manitoba, and probably also northern Ontario. The limits of this form's range are extremely uncertain. Migratory, wintering in eastern Texas, less frequently in western Loui-

siana, western Texas, and eastern New Mexico (Aldrich, 1979). A transitional race, essentially linking *canadensis* with *tabida*, and considered by Tacha (1981) as questionably distinct.

*G.c. tabida*: Greater sandhill crane. Breeds in the United States and southern Canada south of *rowani*, from southwestern British Columbia south to northern California and northern Nevada, in the Rocky Mountain region south from Montana to northern Colorado, in the central plains and Great Lakes region from southern Manitoba and northern Minnesota to central Wisconsin and southern Michigan, and also southeastern Ontario. The range possibly also extends to northern Ontario, but this area's birds are probably closer to *rowani* (Walkinshaw, 1973). Migratory, with the Great Lakes population wintering in Florida, those in the Rocky Mountain population wintering along the Rio Grande in New Mexico and in northern Chihuahua, and the westernmost breeding populations wintering in California, including the Central and Imperial Valleys.

*G.c. pratensis*: Florida sandhill crane. Resident in southern Georgia, from the Okefenokee Swamp (Charlton and Ware counties) to Florida, and in Florida mostly from Alachua and Putnam counties south to the Everglades. Cranes reported from southern Alabama may be of this form or of *pulla*.

*G.c. pulla*: Mississippi sandhill crane. Resident in southeastern Mississippi (Jackson County), and probably formerly also in southern Louisiana.

*G.c. nesiotes*: Cuban sandhill crane. Resident on the Isle of Pines and western Cuba, with the latter population now nearly extirpated.

**Measurements.** Wings of male *canadensis* average 469.9 mm (range 418-510 mm), those of *tabida* 539.7 mm (460-598 mm), of *pratensis* 501.1 mm (460-533 mm), and of *nesiotes* 480.5 mm (460-533 mm).

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Females of *canadensis* average 447.6 mm (420-500 mm), of *tabida* 485 mm (467-510 mm), of *pratensis* 477.9 (445-517 mm), and of *nesiotes* 440.8 mm (425-460 mm). Exposed culmens of male *canadensis* average 92.6 mm (69-110 mm), those of *tabida* 138.6 mm (116-159 mm), of *pratensis* 127.7 mm (113-144 mm), and of *nesiotes* 116.6 mm (115-118 mm). Females of *canadensis* average 91.8 mm (80-103 mm), of *tabida* 131.2 mm (113-147 mm), of *pratensis* 123.3 mm (110-142 mm), and of *nesiotes* 110.4 mm (100-122 mm). Tarsi of male *canadensis* average 189.3 mm (156-228 mm), of *tabida* 244.2 mm (225-265 mm), of *pratensis* 244.6 mm (223-264 mm), and of *nesiotes* 216.3 mm (206-232 mm). Those of female *canadensis* average 181.8 mm (162-212 mm), of *tabida* 231.4 mm (222-240 mm), of *pratensis* 236.3 mm (220-257 mm), and of *nesiotes* 200.0 mm (187-218 mm) (Walkinshaw, 1949). Aldrich (1979) provided comparable data for *rowani*. Wings of males average 497.3 mm (482-525 mm); females 474.25 mm (456-492 mm). Exposed culmens of males average 118.6 mm (109-127 mm); females 103 mm (93-114 mm). Tarsi of males average 226.8 mm (203-240 mm); females 212.25 mm (210-215 mm). Eggs of *canadensis* average  $90.45 \times 57.32$  mm; of *tabida*  $96.24 \times 61.00$  mm, of *pratensis*  $92.46 \times 59.33$  mm, of *pulla*  $95.96 \times 58.55$  mm, of *nesiotes*  $87.94 \times 57.13$  mm, and of *rowani*  $91.69 \times 59.27$  mm (Walkinshaw, 1973).

**Weights.** A sample of 15 adult males and 19 adult females of *rowani* averaged 4,079 and 3,775 grams respectively, while 27 adult males and 25 adult females of *canadensis* averaged 3,746 and 3,355 grams (Lewis, 1979a). The average weight of 46 adult males of *canadensis* shot during winter in New Mexico was 3,515 grams, and that of 50 adult females was 3,203 grams (Boeker, Aldrich, and Huey, 1961). Six males of *tabida* averaged 5,385 grams (range 4,762-5,895 grams) and four females averaged 4,308 grams (range 3,628-4,988 grams). One female of *pratensis* weighed 3,741 grams, and two males weighed 4,081 and 4,988 grams (Walkinshaw, 1973). Adult males of *rowani* range from 3.5 to 5.2 kilograms, and adult females from 3.4 to 4.5 kilograms (Tebbel and Ankney, 1979). Hand-reared birds at 70 days of age averaged 2,823 grams in *rowani*, 2,982 grams in *canadensis*, 3,086 grams in *pratensis*, and 3,268 grams in *tabida* (Archibald and Viess, 1979). The estimated egg weights are 158 grams (*nesiotes*), 164 grams (*canadensis*), 178 grams (*rowani*), 180 grams (*pratensis*), 189 grams (*pulla*) and 204 grams (*tabida*). Egg weights of *canadensis* averaged 138.3 grams, of *rowani* 173 grams, of *pulla* 147.9 grams, of *pratensis* 164.4 grams, of *nesiotes* 133.2 grams, and of *tabida* 196.19 grams; of these only the weights of *tabida* are

specifically of fresh eggs. Weights of chicks include six *pratensis* and *pulla*, averaging 101.1 grams, 4 probable *rowani*, averaging 107.7 grams, and 58 *tabida*, averaging 115.1 grams (Walkinshaw, 1973).

### Description

*Adults of both sexes* are alike, with a bare reddish forehead, lores, and crown to just below the eyes, with sparse blackish bristles. The cheeks, ear coverts, chin, and upper throat are white to pale gray. The nape is pale gray to whitish, and the mantle, scapulars, upper wing coverts, tertials, and tail are pale slate gray, the feathers darker toward their tips. The back, rump, tail coverts, and underparts are pale ashy gray to brownish gray, the feathers broadly fringed with pale ashy gray. The wing feathers are ashy gray to dark slate, the latter color including the primaries, greater primary coverts, and alula. Especially in summer, much of the plumage is often heavily stained with rusty, except on the head and underwing. The iris is reddish to brownish, the bill is dull gray to olive gray, and the legs and toes are blackish.

*Juveniles and immatures* during the first autumn and early winter are similar to adults, but many of the body and wing feathers are washed with ocher or tawny toward their tips, and the head and upper neck area are pinkish to cinnamon. The crown, occiput, and nape are covered with tawny feathers, and there are short gray feathers on the forehead. The tertials are shorter than in adults but are molted by early winter, and from autumn onward the new plumage of the neck and head are essentially grayish, with cinnamon tips. The iris is gray brown to reddish brown. Immatures in late winter and early spring have partially to mostly bare foreheads, and the rest of the plumage is also adultlike, with only scattered brownish juvenile feathers on the wings and body. By this time there has been a complete molt except for the primaries, secondaries, some wing coverts, and the rectrices. Rust-stained feathers of adults may resemble the partially tawny wing coverts of juveniles, but the staining of adults lacks patterning, while that of juveniles often forms distinct patterns (Lewis, 1979d). *Second-year immatures* from autumn to spring resemble adults, but have some old brown feathers retained on the body and upper wing surface, and may also retain some juvenile flight feathers (Cramp and Simmon, 1980; Lewis, 1979d).

*Downy chicks* are generally tawny, becoming burnt sienna on the occiput and light buffy white or light gray on the sides of the face and the forehead, with a darker line beneath the eye, enlarging to a spot on the lores. A dark brownish area extends from the occiput to the rump. The throat is white, and the breast and underwings are dull grayish white. The bill is dull flesh, and the legs and toes are initially flesh-colored, while the

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iris is brown. By about 50 days, the bill is pinkish buff, with a vinaceous cinnamon base, and the legs and toes are a darker pinkish buff (Walkinshaw, 1973). Fledging occurs at about 70 days in the greater sandhill crane (Walkinshaw, 1949), and probably in not less than 60 days in the lesser (Boise, 1976).

### Identification

*In the field*, this is the common wild crane of North America, and is almost uniformly light gray, with a reddish crown patch and black legs, and whitish cheeks. Its calls are rattling, and fairly high-pitched in the lesser sandhill, but louder and more resonating in the larger races.

*In the hand*, this is the only uniformly gray-bodied crane that is totally feathered on the head except for the crown. Its trachea is coiled inside the sternum.

## DISTRIBUTION AND HABITATS

### Historic Breeding Range

Walkinshaw (1949) has summarized the historical status of the major sandhill crane populations of North America. Little can be said of the lesser sandhill crane's historic range, since Walkinshaw was able to find only a handful of breeding records prior to 1920 (ranging from the tip of the Chukotski Peninsula of the USSR to eastern Baffin Island), which collectively would suggest that there have been no major range changes since that time. The breeding range is now known to extend considerably farther west in the USSR than is indicated by Walkinshaw's map, but this is possibly the result of improved information rather than actual range changes. According to him (1973) the subspecies' known breeding range extends from Wrangell Island and extreme northeastern Siberia, across much of western Alaska, some of the Aleutians, south possibly to northern Kamchatka and Cook Inlet, Alaska, and east across Canada to Banks, Victoria, and Southampton Islands, and south to southern Mackenzie, Keewatin, western Hudson Bay, and possibly to the Hudson Bay drainage of western and northern Ontario. Most of these areas represent arctic tundra habitats.

At the time of Walkinshaw's monograph on the sandhill cranes, the Canadian sandhill crane was still undescribed, and his later (1973) description of this race assigned the birds of intermediate size between lesser and greater sandhill cranes to this race, most of which in his opinion probably breed in central Saskatchewan, central Alberta, or central Manitoba, and possibly also nest in eastern British Columbia or northern Ontario. The indefinite morphological limits of this subspecies

make it impossible to judge its previous or current range limits. Aldrich (1979) reviewed over 400 specimens and concluded that the form's known range occurs in aspen parklands and boreal forests from central southern Mackenzie District and central Alberta eastward through northern and central Saskatchewan, central Manitoba, and northern Ontario to James Bay. The limits may also extend farther to the northwest than available records indicate.

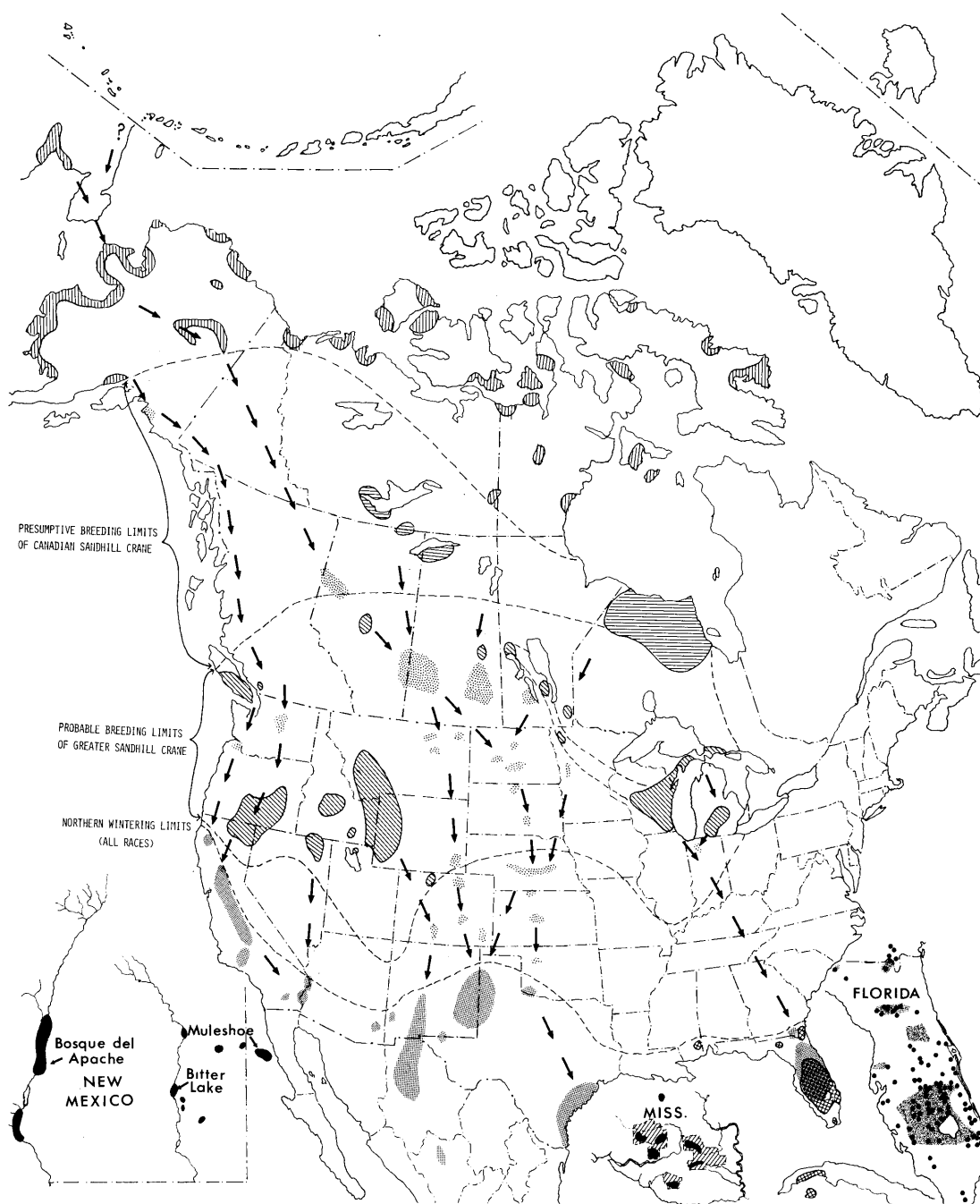
Walkinshaw (1949) reported that the greater sandhill crane was formerly found throughout southern British Columbia, central and southern Alberta, Saskatchewan, northern Manitoba, southwestern Ontario, and Michigan south to northeastern California, northern Nevada, Arizona, northern Utah, northwestern Colorado, Nebraska, Iowa, Illinois, Indiana, and central Ohio. It disappeared from many of these areas in the late 1800s and early 1900s, disappearing as breeding birds from Nebraska in the 1880s and from Arizona about 1910. They also became extirpated as nesting birds from South Dakota (1910), Iowa (1905), Illinois (1890), Indiana (1929), and Ohio (1926), and virtually disappeared from North Dakota, where single pairs have been observed breeding at rare intervals. It is not known when they disappeared from southwestern Ontario, where they were apparently rare nesters even in early days (Walkinshaw, 1949), and have evidently recently reinvaded.

The Florida sandhill crane formerly bred as far west as southern Louisiana. The birds were probably never common in Alabama, where they were last reported nesting in 1911, and once occurred northward to southern Georgia, from Okefenokee Swamp to Wakulla County. The crane population of the Okefenokee Swamp dwindled until the area was made into a refuge in 1936, and thereafter began a slow increase (Walkinshaw, 1949).

Nothing is known of the historical range of the Mississippi sandhill crane, which was not formally described until 1972. It is possible that the birds breeding in southern Louisiana were of this species, and even more probably the population of southern Alabama may have belonged to this subspecies. Cranes with chicks were seen in southern Louisiana as late as 1918. They were found nesting in Mississippi in 1938, but it was not until the 1960s that the birds were suspected to be a distinct subspecies. By that time the total population was believed to number less than 50 birds, and the entire breeding range was determined to be limited to the area between the Pascagoula River and the Harrison-Jackson county line (Walkinshaw, 1973; Valentine and Noble, 1970).

The historical status of the Cuban sandhill crane is also extremely obscure. However, all of the available nesting records are from the Isle of Pines (Walkinshaw, 1973). It also probably was a resident of the provinces of

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Breeding ranges of the lesser (vertical hatching), Canadian (horizontal hatching), and greater (diagonal hatching) sandhill cranes, and residential distributions of Mississippi, Florida, and Cuban sandhill cranes (cross-hatching). Fine shading indicates major wintering areas of migratory races, and coarse stippling indicates migratory staging areas. Insets show locality records and concentration areas (stippled) of Florida sandhill cranes, breeding areas (and associated refuge limits) of Mississippi sandhill cranes, and wintering concentration areas in New Mexico.

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Pinar del Rio, Habana, Matanzas, Santa Clara, and western Camaguey (Walkinshaw, 1949).

### *Current Breeding Range*

Presently it is believed that the lesser sandhill crane still nests over most or all of its historical range in North America, from western Alaska to the Hudson Bay area of Canada. The Siberian breeding population has recently been found to be considerably larger than had been generally appreciated. As early as 1909 the birds were observed in pairs during summer as far west as Kilyuchin Bay, and in the early 1970s were found to be a common nester in that general area (Krechmar, Andreev and Kondrat'ev, 1978). It is not yet known to be a definite nester on Wrangel Island (Portenko, 1981), although pairs or individuals have been observed summering as far west as the Indigirka River. The total Soviet population probably now numbers about 20,000 individuals and may still be dispersing westward (USSR Crane Working Group Information Bulletin No. 2, 1981). Its eastern breeding limits in North America are apparently on Baffin Island, where it is rare, and in the vicinity of Churchill, Manitoba (Walkinshaw, 1981a).

The current known range of the Canadian sandhill crane was described in the previous section.

Walkinshaw (1981a) has summarized the present known breeding range and status of the greater sandhill crane. Little is known of the British Columbia segment, but a few are known to nest at Pitt Meadows. In Oregon the birds nest in Malheur, Harney, Lake, Grant, Baker, Union, Deschutes, and Klamath counties, and in California in Modoc, Lassen, Siskiyou, Sierra, Plumas, and Shasta counties. This population winters in California and consists of some 3,000 to 3,200 birds, exclusive of any from British Columbia and Washington (Littlefield and Thompson, 1979).

The Nevada breeding population is centered in Elko County, and the birds winter along the Colorado River near Poston, Arizona (Drewien, Oakleaf, and Mullins, 1976). This population probably consists of more than 1,000 birds.

The major Rocky Mountain population nests from northeastern Utah northward along the Idaho-Wyoming border to southwestern Montana, and in the early 1970s was estimated to consist of some 10,000 to 15,000 birds (Drewien, 1973). A small extension of this population, of about 250 birds, also occurs in northwestern Montana in Routt, Moffat, and Jackson counties (Beiniasz, 1979).

There was a single breeding record of sandhill cranes in North Dakota in 1973 (Johnson, 1976), but this state must still be considered extralimital for sandhill crane breeding. In Minnesota there were about 70 pairs plus nearly 150 nonbreeders in 1977, scattered over Anoka,

Aitkin, Beltrami, Chisago, Kanabec, Lake of the Woods, Mahanomen, Marshall, Mille Lacs, Morrison, Kittson, Pine, Sherbourne, Pennington, Polk, and Roseau counties (Grewe, 1977).

The current status of the sandhill crane in Wisconsin has improved from a situation of perhaps as few as 25 pairs present in 1936 to an estimated 1,000 birds in 1973, including 250 pairs in 32 counties (Hunt and Gleusing, 1976). In the late 1970s nesting was reported from northeastern Illinois for the first time in this century (Walkinshaw, 1981b).

The Michigan population now includes an Upper Peninsula segment of about 130 pairs occurring over some 218 square miles of the eastern part of the peninsula (Tayler, 1977). Walkinshaw (1978) recorded crane nests from Alger, Baraga, Chippewa, Delta, Luce, Mackinac, and Schoolcraft counties, and observed a general trend of population increase and spread in recent years. The birds have also recently moved into adjacent Ontario, where they are again nesting (Tebbel and Ankney, 1979), and have spread south into the Lower Peninsula, breeding as far as Cheboygan County and possibly to Mason County (Walkinshaw, 1981b). Elsewhere on the Lower Peninsula, Walkinshaw (1981b) reported cranes nesting since 1930 in Mason, Clinton, Shiawassee, Barry, Eaton, Ingham, Livingston, Kalamazoo, Calhoun, Jackson, Washtenaw, St. Joseph and Branch counties, and during the past few years nests have also been found in the southern tier of Michigan counties.

Evidence of the great increase in greater sandhill populations in the eastern states comes from surveys of fall populations at the Jasper-Pulaski Game Area, in northwestern Indiana, where the birds increased from 35 in 1935 to about 14,000 by the fall of 1979. This area is the only known major fall staging ground for the eastern population, and probably includes birds from breeding areas in Michigan, Wisconsin, Minnesota, Ontario, and perhaps Manitoba (Shroufe, 1976).

The population of the Florida sandhill cranes has recently benefited from improved protection, and probably numbers at least 5,000 birds. Many of these are in large refuges, including Okefenokee National Wildlife Refuge, in Georgia, and Payne's Prairie (Alachua County), Three-lakes Wildlife Area (Osceola County), Avon Park Wildlife Area (Polk and Highland counties), Fish-eating Creek Wildlife Management Area (Glades County), and Loxahatchee National Wildlife Refuge (Palm Beach County). However, the other old breeding areas are disappearing as a result of human use, and thus the situation is a mixed one (Walkinshaw, 1981b).

In Mississippi, the crane population continues to remain at a low but stable level of about 40 to 50 birds, but has been helped by the establishment of the Mississippi Sandhill Crane National Wildlife Refuge

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in 1974. Twenty nesting territories have been located since 1965, but at least nine have apparently been deserted (Valentine, 1979).

No new information on the status of the Cuban sandhill crane is available, but Walkinshaw believed that in the early 1950s there were probably 100 birds on the Isle of Pines, with the greatest concentration near Los Indios. The mainland population was then probably much lower, but has more recently begun to increase or at least has remained stable (Walkinshaw, 1981a).

### *Breeding Habitat Requirements and Densities*

Breeding habitats of the lesser sandhill crane are lowland tundra and associated marshes, shorelines of rivers, lakes, and coastal areas, and grassy slopes up to about 1000 meters elevation. In some areas, such as on southern Banks Island, in arctic Canada, the birds nest on grass-covered sand dunes, and they also often nest in muskeg areas where there are open, sedge or moss-covered areas surrounded by spruces and with scattered bushes present (Walkinshaw, 1973). On the Yukon-Kuskokwim Delta the birds were found nesting on two general habitat types, heath-marsh mosaic tundra areas and sedge-grass meadows. Most nesting occurs in wet marshes of the mosaic tundra areas and in the sedge-grass meadows, but extends onto dry heath tundra. Nesting density was found to range from 0.54 to 0.74 nests per square kilometer during two years of study, with aerial surveys suggesting a minimum density of 1.5 birds per square kilometer over a 1,250 square kilometer area (Boise, 1977).

The Canadian sandhill crane nests in inaccessible bulrush marshes or muskeg areas vegetated with dwarf birches (*Betula pumila*) and tamaracks (*Larix laricina*). In Mackenzie District the birds appear to prefer extensive bulrush cover and associated shallow marshes, while in the James Bay area of Ontario they have been observed nesting in sphagnum bogs, among tamaracks and associated heather vegetation. This general sort of vegetation is scattered but widespread across western and central Canada, allowing for a dispersed but fairly substantial total population (Aldrich, 1979). Carlisle (1982) has described the sedge-marsh nesting habitats of sandhill cranes in central Alberta, which may be referable to this race.

The greater sandhill crane's breeding habitats in the western states consist of open mountain parks in coniferous forests, willow-dotted streams in sagebrush areas, extensive shallow freshwater marshes in sagebrush or arid grasslands, beaver ponds and associated wetland habitats, and other similar habitats. Their densest known concentrations occur at Gray's Lake, Idaho, where about 200 pairs nest within an area of about 10,000 hectares, and territory sizes average only about 17

hectares (Drewien, 1973). By comparison, territories at Malheur National Wildlife Refuge in Oregon were estimated to average about 25 hectares (62 acres), according to Littlefield and Ryder (1968).

Walkinshaw (1973) judged that in Michigan the territories he studied on the Lower Peninsula have averaged about 53 hectares (132 acres) and those on the Upper Peninsula about 85 hectares (210 acres). He believed that an essential territorial component is fresh water (pH 5.0-7.6), with preferred depths of from a few inches to two or three feet near the nesting site. The plant cover usually consists of sedges (*Carex*), grasses, cattails (*Typha*), rushes (*Scirpus*), and reeds (*Phragmites*), at least in southern Michigan and Wisconsin. However, in northern Michigan the typical breeding habitat consists of bogs, with associated heath vegetation (*Ledum*, *Kalmia*, *Andromeda*) and such trees as tamaracks, pines, and black spruce (*Picea mariana*). Generally nesting densities are quite low; Taylor's (1977) estimate of 130 pairs in 56,486 hectares suggests an overall density of a pair per 434 hectares over large areas. Walkinshaw (1981a) stated that although cranes in Michigan only used larger (324-810 hectare) marshes during the early years of his studies, they recently have begun to move into smaller marshes, including some less than 5 hectares in area.

The Florida sandhill crane nests in pond areas associated with prairies dominated by saw palmettos (*Serenoa repens*) and scattered wooded hammocks that support cabbage palms (*Sabal palmetto*), pines, oaks, and wetland trees such as magnolias and cypress (*Taxodium distichum*). Most nesting apparently occurs on shallow-water ponds grown up thickly to emergent vegetation such as pickerelweed (*Pontedaria*), bog-button (*Lachnoculon*), pipewort (*Ericaulon*), goldies (*Xyris*), rushes (*Juncus*), arrowleaf (*Sagittaria*), maidencane (*Panicum*), saw-grass (*Cladium*), cattail (*Typha*), and spike rush (*Eleocharis*). The average pond size of nests studied by Walkinshaw was 3.9 hectares, ranging from 0.2 to 18.2 hectares. However, at the Loxahatchee Wildlife Refuge the birds nest mainly in an area where the wet prairie "tree island" zone is located within a surrounding wet prairie matrix of sawgrass and slough communities (Walkinshaw, 1973). In the central area of Florida the nesting population of cranes was estimated by Walkinshaw (1976) to consist of from 96 to 107 pairs of birds on 123,000 hectares in 14 different sites, suggesting a general density of about a pair per 1,200 hectares. Excluding land that does not provide suitable crane habitat, the actual density was probably about twice that great, and the pairs tended to be separated by average distances of about 1.6 kilometers.

Studies of the Mississippi sandhill crane by Valentine (1979; 1981) indicate that about 20 territories (some of which have been abandoned) occur on 11 general areas in Jackson County. Nesting habitats consist of swamps



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and prairie-like savannas surrounded by natural pine forests or pine plantations. The planting of trees on most of the native savanna has restricted the breeding range recently, as has natural succession of brush, bald-cypress, and pines, which tend to close over the swamp savanna vegetation. Density estimates are not available, but one swampy area of about 324 hectares supported three nests in one year, and another area of 364 hectares supported two nests in one year. One small savanna only about 4 hectares in area, surrounded by swamp and pine forests, also supported a nest territory one year (Valentine, 1981). Generally the habitats and territorial requirements of this form would seem to be very much like those of the Florida race.

In Cuba, the birds nest in relatively dry habitats that are typically parklike and sparingly grown to shrubs and trees, although some open prairie habitat does occur. Nests have been found on dry ground, as in bottle palm (*Colpothrinax*) flats along grass-covered arroyos, or in dry and sandy lowland situations, with an abundance of dead grasses and scattered trees such as tropical pines, palmettos, (*Acoelorrhaphe*) and various shrubs (Walkinshaw, 1973). In one area Walkinshaw found eight pairs in an area of 3,108 hectares (a pair per 388 hectares), while in another he found three pairs in an area of two square miles (a pair per 173 hectares). No other comparable concentrations were found by him.

### *Wintering Range and Habitats*

Walkinshaw (1949) described the wintering range of the lesser sandhill crane as extending from central California, central New Mexico, and the panhandle of Texas south at least into Baja California, San Luis Potosi, and Jalisco, and perhaps as far south as the Central Valley of Mexico. About 20,000 to 23,000 currently winter in the Central Valley of California, especially in San Joaquin County (Littlefield and Thompson, 1979). The largest numbers of sandhill cranes wintering in Mexico are probably found in Chihuahua (Lewis, 1977), and no significant numbers are known to winter in northeastern Mexico to the south of their known wintering areas in southern Texas (Aldrich, 1979). However, the major concentration areas for many decades have been Bitter Lake National Wildlife Refuge, in Chaves County, New Mexico, and Muleshoe National Wildlife Refuge, in Bailey County, Texas. The wintering flock at Bitter Lake dates back at least to the 1940s, when about 11,000 birds were known to winter there. Similar numbers of 8,000 to 15,000 were also present during the same period at Muleshoe Refuge, while smaller numbers wintered along the Texas coast, including about 1,500 in the Aransas area (including unknown numbers of Canadian and greater sandhill cranes).

Recent studies of the birds wintering on the coast of

Texas indicate that lesser and Canadian sandhill cranes winter all along the Texas coast from the Mexican border to Houston, while the greater sandhill winters mainly from Aransas County eastward. The total wintering population in the early 1970s was estimated to be approximately 4,350 lessers, 15,550 Canadian, and 2,000 greaters (Guthery and Lewis, 1979). It is thus apparent that the majority of the lesser sandhill cranes winter in interior Texas and adjacent New Mexico.

Buller (1979) summarized late fall population survey data of sandhill cranes in eastern New Mexico and western Texas taken from 1960 to 1976 and indicating peak concentrations in these two states that usually ranged between 110,000 and 340,000 birds, with very large year-to-year differences. Some of the areas in New Mexico where the birds roost during winter in addition to the Bitter Lake area include Lewiston Lake, Salt Lake, Bottomless Lakes, Dexter Slough, and the Ft. Sumner area of Pecos River. Major wintering areas in western Texas besides Muleshoe Refuge include Rich Lake, Mound Lake, Double Lakes, Cedar Lake, Coyote Lake, and Baileyboro Lake (Boeker et al., 1961). Nearly all of these winter roosting areas are shallow, alkaline lakes with grain sorghum fields nearby in which the birds forage. A substantial number of sandhill cranes also winter in the Central Highlands of Mexico; Buller (1982) reported from 5,745 to 33,315 birds in 1977-1981 surveys.

It is likely that a substantial percentage of the cranes currently assigned to the Canadian race winter along the Gulf Coast of Texas, since, as mentioned earlier, an estimated 15,550 of the cranes studied in the Gulf Coast area by Guthery and Lewis (1979) were judged to be of the Canadian race, or about 70 percent of the total wintering population. Populations of at least 1,000 birds were reported from Fort Brent, Colorado, Wharton, Matagorda, Lavaca, Jackson, Calhoun, Karnes, Arkansas, Kellberg, Hidalgo, and Cameron counties. While wintering in coastal Texas the birds concentrate in coastal areas and a short distance inland, feeding in such habitats as ephemeral ponds and marshes, coastal scrub oak, and post oak savanna. They also forage in agricultural fields of rice, sorghum, and a few other crops, but the most important energy sources for the birds are native plants, especially nutgrasses (*Cyperus*), with rice and sorghum of secondary importance (Guthery, 1976). Favored wintering habitats in southern Texas typically consist of large and fairly inaccessible bodies of water, broad tracts of land in native vegetation, and nearby fields under intensive crop production (Aldrich, 1979).

Wintering areas of the greater sandhill crane are widely scattered. The Central Valley of California supports about 3,000 birds, in an area extending from about 10 miles southwest of Chico, Butte County, south and east to near Delano, Tulare County. The largest

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numbers winter just south of Thornton, in San Joaquin County, with Butte County supporting the next largest concentrations. Progressively smaller numbers winter in Stanislaus, Merced, and Tulare counties (Littlefield and Thompson, 1979).

Eastward, the central Rio Grande Valley, particularly the vicinity of Bosque del Apache National Wildlife Refuge in New Mexico, is a major wintering area for birds of the Rocky Mountain population (Drewien, 1973; Drewien and Bizeau, 1974). Few, if any, of the cranes wintering in the eastern counties of New Mexico and the western counties of Texas are of the greater subspecies (Boeker et al., 1961). However, a few greater sandhill cranes winter along the eastern coast of Texas, especially from Aransas County eastward, where perhaps 2,000 birds of these races were judged present in the early 1970s (Guthery and Lewis, 1979). There is also a small wintering flock of sandhill cranes in coastal Louisiana (Smith, 1979), although their subspecific identity is not yet known.

Greater sandhill crane wintering areas in Florida have recently been studied by use of radio-tracking methods (Toepler and Crete, 1979), and 22 use areas supporting over 4,000 cranes have thereby been located in that state. All these roosts were shallow freshwater wetlands within 9.6 kilometers of wetland and upland foraging areas, and they extend from Baker and Lafayette counties in the north to Indian River and Highland counties in the south. Among the most heavily used sites were Emerald Marsh, Lake County; Church Lake Prairie, Marion County; Rhodes Dairy, Lake County; and James Hill Farm, Highland County, all of which supported in excess of 300 birds during the period of study. Probably the most important single wintering area is Payne's Prairie, Alachua County (Williams and Phillips, 1972).

## FOODS AND FORAGING BEHAVIOR

### *Foods of Adults*

Some information on the seasonal foods of sandhill cranes may be found in table 7; this table includes immature birds as well as adults, and includes birds representing the greater (Idaho), lesser (Nebraska), and Canadian (Texas) races. There is little reason to believe that any significant differences exist in the races as to preferred foods, and it is evident that sandhill cranes tend to be able to adjust their diets to the local sources of abundant vegetable foods, especially grain crops when they are available. It is clear that, for example, corn provides the single most important source of food energy among lesser sandhill cranes during their spring stopover in Nebraska, and probably contributed about 96 percent of the total daily food intake per bird during

this important period of their spring migration (Reinecke and Krapu, 1979). Since corn contains only about 10 percent protein, the birds apparently supplement their protein intake somewhat by foraging on various invertebrates, which comprise nearly all of the remaining food materials that the birds consume during this period, according to Reinecke and Krapu. Lewis's (1979a) studies in the same area indicate a similarly high (89 percent) proportion of corn among the dietary components, and he noted that corn has a high net energy value, as much as 80 percent nitrogen-free extract, and it is an excellent food for fattening poultry. Lewis suggested that this high corn diet in spring may be an important factor in the substantial weight gain that the birds put on while in the Platte Valley, and Iverson, Tacha, and Vohs (1982) also suggest that the high energy values of cereal grains are an important aspect of crane survival strategies in winter and spring.

### *Food of Young*

No special studies of the foods of young sandhill cranes have been undertaken, but by the time the young are migrating during the fall they appear to be eating essentially the same foods as the adult birds. None of the several food-analysis studies done on migrating or wintering sandhill cranes has reported any age-associated food intake variations. Walkinshaw (1949) described the food of a chick that he raised as including earthworms and beetles by the time it was three weeks old. It also ate mosquitos, spiders, grubs, moths, millers, and some houseflies. By about a month of age it was very fond of earthworms and would eat as many as 400 in a single day. At this time it was also eating crickets, katydids, and short-horned grasshoppers on an everyday basis, as well as other foods.

When over three months old it began to eat sweet corn, and within a week was eating an ear per day. Later in the fall it consumed mainly scratch food such as wheat and cracked corn, but it also consumed fruit and vegetables such as carrots, lettuce, and celery. Walkinshaw summarized information on the food of dependent young wild cranes, suggesting that earthworms are probably an important source of food under natural conditions, and that grasshoppers and other insects are also probably eaten regularly.

### *Foraging Behavior*

Sandhill cranes forage primarily on land, and do a great deal of digging with their bills when necessary to extract materials from under the soil. More often, they feed on visible food from the soil's surface. Large pieces of food, including live prey, are broken into smaller bits by piercing them or threshing them against the ground. Smaller pieces of food are delicately picked up from the ground with the tip of the bill, then tossed into the air

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and caught farther back in the bill, where they can be more readily handled and swallowed (Walkinshaw, 1949; 1973).

### MIGRATIONS AND MOVEMENTS

#### *Seasonal Movements*

Walkinshaw (1949, 1973) described the migratory patterns of both greater and lesser sandhill cranes in great detail, and rather little needs to be added to update his very complete summaries. The migration of the lesser sandhill crane from Siberia and the northernmost portions of Canada begins in late August, reaches a peak during the third week of August, and after the middle of September begins to decline, until the last birds leave after mid-October (Stephen, 1967). At about the same time large numbers of birds build up in North Dakota, especially in Kidder, Stutsman, and McLean counties, with smaller numbers in various areas of eastern Montana (Bowdoin, Medicine Lake, and C.M. Russell National Wildlife Refuges). The birds move southward across eastern Wyoming and the western parts of South Dakota and Nebraska to eastern Colorado and central Kansas, with birds arriving in the Arkansas Valley by mid-September to mid-October and in various refuges of Kansas (Kirwin, Quivira) between mid-October and late November. A few areas in Oklahoma (Salt Plains and Washita National Wildlife Refuges, as well as the Red River bottoms) are usually stopping points before the birds arrive in the New Mexico, Texas, and Chihuahua wintering areas (Buller, 1967).

The spring migration takes a rather different form, with the vast majority if not virtually all of the lesser sandhills wintering east of the Rocky Mountains stopping in the Platte Valley of Nebraska for approximately six weeks, from late February or early March until the second week of April (Frith, 1974, 1976). During that period perhaps all but the approximately 20,000 or so lessers wintering in California, or at least 90 percent of the entire lesser sandhill crane population, are concentrated into a relatively few river miles (U.S. Fish and Wildlife Service, 1981). Spring surveys along the Platte River between 1959 and 1978 indicate peak populations of from about 80,000 to 225,000 birds, averaging nearly 160,000, although a few larger estimates of the mid-continental sandhill crane population have been made, such as Lewis (1979b), who believed that the number of birds in the entire Central Flyway area approached 400,000 in 1976, which would include both lesser and Canadian sandhill cranes. In any case, after the birds leave Nebraska in the first half of April they begin to spread out, and there is no comparable staging area farther north during the spring migration.

The migration routes of the Canadian race are still

only very poorly understood, but it is believed that virtually all these birds also have their spring staging area in Nebraska as well (Krapu, 1979). Lewis (1979a) judged that the Canadian race is more abundant at the eastern end (Overton to Grand Island area) of the central Platte Valley, while the lessers are more common to the west. A few greater sandhill cranes may also stop along the Platte Valley between Wood River and Chapman, perhaps from the population nesting in Manitoba and wintering in eastern Texas and Oklahoma. Most of the birds that stop in the Platte Valley must still fly anywhere from 1,280 to 5,440 kilometers (795-3,380 miles) to reach their nesting areas, and thus the fattening process that they undergo there may be of particular importance to their physical condition at the critical time of reproduction (Lewis 1949a).

Three major migratory routes are known for the greater sandhill cranes. One leads from nesting areas in Oregon and California to relatively nearby wintering areas in California (Littlefield and Thompson, 1979). A second extends from the northern Rocky Mountain breeding population concentrated in Idaho, Montana, and Wyoming to wintering areas in the central Rio Grande Valley of New Mexico, with a stopover in the San Luis Valley of southern Colorado (Drewien and Bizeau, 1974). The third route, probably followed by all of the greater sandhill cranes nesting from Minnesota to Michigan and adjoining areas, funnels initially into the Jasper-Pulaski Fish and Wildlife area near Medaryville, Indiana (Shroufe, 1976), and then continues more or less directly southeastward across Kentucky, Tennessee, Georgia, and on into Florida (Toepler and Crete, 1979; Nesbitt and Williams, 1979). The return route in spring is probably very similar to the fall route (Williams and Phillips, 1972), although less extensive use of the Jasper-Pulaski area occurs at that time of year.

The remaining populations, the Florida, Mississippi, and Cuban sandhill cranes, are all believed to be essentially sedentary.

#### *Daily Movements*

Studies by Toepler and Crete (1979) on radio-tagged greater sandhill cranes indicated that at least five birds flew some 584 kilometers in 9.5 hours (from Chattanooga, Tennessee, to Impassible Bay, Florida) without stopping. During spring migration, one pair of birds migrated 850 kilometers in 55 hours, and made two overnight stops en route from the Jasper-Pulaski area to its breeding marsh in central Minnesota. The birds seemed generally to migrate during clear to partly cloudy weather, flew from 272 to 484 kilometers per day, and landed before sundown. Only a few birds migrated into headwinds or crosswinds, and most apparently migrated at altitudes of from 50 to 1000 meters. Melvin

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and Temple (1982) stated that most migration occurs within 1,600 meters of the ground, and that daily flights of 48 to 740 kilometers have been documented.

### GENERAL BIOLOGY

#### *Sociality*

Information on relative sociality in sandhill cranes can be extracted from average flock sizes under various conditions. Walkinshaw (1949) reported flock sizes of lesser sandhill cranes leaving and arriving at winter roosts in eastern New Mexico and Texas. His data would suggest that flocks leaving roosts at dawn average from 16 to 20 birds, while similar counts made during return flights to roosts in evening indicate average flock sizes of about 35 birds. These sizes are, of course, highly variable, and it is probable that in part they reflect relative security; the largest flock sizes seem to be those associated with wintering birds in refuge areas. By comparison, Bliese (1976) reported daytime flock sizes in spring during the birds' stopover period in the Platte Valley. These counts, made of standing and flying birds in field-feeding situations, indicate a much smaller flock size, with over 77 percent of the flocks having 50 or fewer birds, and 84 percent having no more than 100. The most common social units reported by Bliese were groups of two birds (11.7 percent of the total) and three birds (9.6 percent), supporting the general idea that the pair and family group are probably the nuclear units of crane flocks.

#### *Daily Activities*

In sandhill cranes the daily flights to and from roosts are closely tied to light levels. Walkinshaw's (1949) data on morning and evening flights at the Bitter Lake National Wildlife Refuge, for example, suggest that most birds left the roost shortly after sunrise, and there was a massive evening return immediately around the period of sunset. Almost certainly light levels, rather than sunrise or sunset per se, are the critical factor, for in the Platte River area the cranes always begin returning to the river before sunset on cloudy days, but often wait until a half hour or later beyond sunset on sunny days with extended periods of twilight.

When foraging, the birds tend to form generally linear flock shapes, although this is quite variable, and many other flock conformations also occur (Bliese, 1976).

#### *Interspecific Interactions*

Walkinshaw (1949) judged that only a few predators probably affect nesting success of lesser sandhill cranes,

including such types as wolves, foxes, dogs, jaegers, hawks, eagles, and owls. He believed that jaegers (*Stercorarius* spp.) might be the most significant avian egg predator of the lesser sandhill crane, and that crows and ravens might also be significant predators, at least for greater sandhill cranes. Among Florida sandhill cranes, raccoons are probably the most common predator of nesting birds, although various snakes and crocodiles might perhaps also pose a danger. There are no wild mammalian predators such as wolves or foxes in Cuban sandhill habitats, and very few dogs; Walkinshaw pointed out that it is under such conditions that the birds can nest successfully in dry areas, apparently requiring water only for drinking.

### BREEDING BIOLOGY

#### *Age of Maturity and Time of Breeding*

The normal age of maturity in the wild is still uncertain, but semen has been obtained from hand-reared male birds that were only three years old (Archibald and Viess, 1979). A pair of sandhill cranes at Flamingo Gardens, in England, initially bred when the male was eight years old and the female six. Johnson (1979) assumed that both sexes of sandhill cranes begin to breed in the wild at four years of age, but this remains to be proven. It is quite possible that a small proportion, particularly males, may be able to breed at four or even three years, but several more years may be needed before all of the birds are successful at mating and establishing territories.

A substantial amount of information is available on the timing of breeding in the various races of sandhill cranes (see table 14), and not surprisingly there is a marked relationship between latitude and the onset as well as the duration of the nesting period, based on available egg records. The more southern populations of sandhill cranes not only begin nesting earlier but also have a much more prolonged egg-laying period. This perhaps reflects a considerable incidence of renesting behavior, although the incidence of renesting in these races is still undetermined. Walkinshaw (1965a) reported that in Michigan he located 82 nests in April, 37 in May, and one each in June and July. He judged that nests found in late May were second nesting efforts; three nests were listed as being found after May 20. Including the two June and July records, this would suggest that under 5 percent of the nests located were likely to have resulted from renesting. Limited studies of the lesser sandhill crane, however, have offered no firm evidence of renesting behavior in that race (Boise, 1977). Three probable cases of renesting have been reported in the Mississippi race (Valentine, 1982).

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### *Pair Formation and Courtship*

Walkinshaw (1965a) reported that little is known of the process of pair formation in cranes, but he judged that it occurred when the birds were about three years old. Thereafter the newly mated pairs probably spend a summer or more on their territories, usually in marshes unoccupied by resident birds. The sandhill cranes return to Michigan in pairs, and these immediately disperse to breeding territories after their spring arrival. Thus, pair-bonding must occur on wintering areas or during the rather brief spring migration.

Current evidence suggests that pair-bonding in this species is similar to that of other cranes, with the unison-call ceremony playing a vital role in the establishment and maintenance of pairs. Archibald's (1975,1976) descriptions indicate that the behavior in this species is significantly different from that of other *Grus* species to warrant its placement in a separate "species-group." In the sandhill crane, both sexes keep their wings completely folded during the display, and the only significant movements are the vertical head movements of the male, performed each time he utters a call-note. Typically the female begins the display with a long, pulsed call sounding something like machine-gun fire, and followed by a prolonged series of short calls uttered in synchrony with slightly longer calls by the male. Occasionally a male will raise his back feathers and also his inner wing feathers while calling during high-intensity threat situations. Both birds typically remain stationary during the entire ceremony.

Copulation in the sandhill crane takes the typical form found in other *Grus* species. Walkinshaw (1973) has observed copulation on several occasions, and noted that it is typically performed on the birds' breeding territories, and in all of five cases it occurred during morning hours. In every case the female approached the male with her head held low and assumed a receptive posture, with her neck extended forward at a 45-degree angle and her wings somewhat extended. The male swiftly approached, and copulated with his wings beating slowly. Littlefield and Ryder (1968) observed copulation on 25 occasions, and noted that it occurred at various times throughout the daytime period. On only two occasions was any dancing behavior associated with copulation, one occurring both before and after, and once only after.

### *Territoriality and Early Nesting Behavior*

Walkinshaw (1965b) studied the territoriality of the greater sandhill crane in Michigan, and reported that the average territorial size of 76 breeding territories in the Lower Peninsula has been 132 acres, while 13 Upper Peninsula territories averaged 210 acres. By comparison, 7 territories of the Florida sandhill crane averaged

about 103 acres, and 4 territories of greater sandhill cranes in Idaho averaged 161 acres. In a dense concentration of birds at Michigan's Phyllis Haehnle Memorial Sanctuary, 7 pairs usually nest each year in an area of only about 260 acres of actual marsh, and the average territory size over a five-year period was estimated by Walkinshaw to be about 43.5 acres. This is somewhat similar to the fairly dense territories reported by Drewein (1973) in the Gray's Lake area of Idaho, where 10 territories averaged 17 hectares (about 42 acres). Such territorial sizes probably approach the minimum generally acceptable to greater sandhill cranes, although Walkinshaw did estimate that some birds occupied territories as small as 8 acres. In the Phyllis Haehnle Sanctuary, the birds not only defended the wet marsh area but also used adjacent dry marsh areas after their young were hatched. When these dry areas are included in the estimates, 71 territories (counting the territories of each pair every year separately) averaged 39.62 acres, and ranged from 8 to 90 acres (Walkinshaw, 1973). Littlefield and Ryder (1968) estimated that the smallest territory in their study area in Oregon was 3 acres, and the largest was 168 acres, with 8 averaging 62 acres.

Walkinshaw (1965a) found that all of 120 greater sandhill crane nests he studied on Michigan's Lower Peninsula plus one in the Upper Peninsula were built in shallow-water marshes, typically among cattails and sedges. Twelve of 13 nests in the Upper Peninsula were built in bogs, usually of sticks and clumps of mosses. In that area, the period of nest construction requires approximately a week, and the nest is constructed by both birds working a few hours each day. Of 26 nests of the lesser sandhill crane studied by Boise (1977), most were on slightly raised mounds in wet marshes. However, the sites used ranged from shallow-water ones to some on dry tundra, and were generally in drier situations than those typical of greater, Florida, and Mississippi sandhill cranes. Relatively dry nest sites were also reported by Walkinshaw (1973) as seemingly typical of the Cuban sandhill crane. Over half of 49 nests in Michigan's Upper Peninsula analyzed by Walkinshaw (1981b) had no standing water beside them, but all were surrounded by water, and all were well isolated from humans. Nests in the Upper Peninsula bogs tend to be smaller than those built in marshes, and some nests built on dry land tend to be very small indeed. The size of the nest is evidently largely a reflection of the amount of water and associated vegetation immediately around the nest, and this is highly variable. Walkinshaw (1965c) noted that one lesser sandhill crane nest he observed on Banks Island merely consisted of a few pieces of willow torn from nearby plants, situated on the highest tundra mound in the vicinity. This nest contained the remnants of egg shells apparently from the year before, indicating that sandhill

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cranes sometimes use the same nest site in subsequent years.

### *Egg-laying and Incubation*

In his Michigan studies, Walkinshaw (1965a) found that the eggs were laid from two to three days apart. As soon as the first egg is laid, incubation begins, and is performed alternately by both members of the pair. The attentive period of the cranes is to some extent regulated by the behavior of the nonincubating bird, since the incubating bird seldom leaves the nest until it is relieved by its mate. Walkinshaw found that male attentive periods averaged 215 minutes for 41 periods, and females averaged 195 minutes for 33 periods. The eggs were always found to be incubated during the night, and in four observed cases this was being performed by the male. The average nighttime attentiveness period for the five nests was 938 minutes. During the daytime hours the nests were found to be incubated for 97.6 percent of the observed time, and slightly over half of this daytime incubation was observed to be performed by the male. Daytime changeovers in incubation duties were found to range from once to seven times, and during 29 observation days the average number of changeovers was 3.6 times. There are evidently no changeovers during the nighttime hours (Walkinshaw, 1965d, 1973).

Loss of clutches prior to hatching have been studied in various crane populations (table 35). In Walkinshaw's (1965a) Michigan studies, he noted that 73.8 percent of 107 nests were successful, and that 68.1 percent of 201 associated eggs hatched. If deserted nests are discounted, young hatched in 78 (81.2 percent) of 96 nests, and 134 eggs (74.4 percent) of a total of 180 hatched. In Michigan, raccoons were found to be the most serious predators of eggs. Raccoons were also

reported to be serious egg predators in Oregon by Littlefield (1976), where coyotes are also present and were found to be minor egg predators but serious sources of mortality of young birds. Coyotes were also reported by Drewien (1973) to be significant predators in the Gray's Lake area of Idaho. Boise (1977) estimated that predators were responsible for the loss of 27.3 percent of the eggs of lesser sandhill cranes in western Alaska, where overall nesting success was estimated at 66.7 percent and hatching success was 63.6 percent. Gulls, jaegers, foxes, and Eskimos were considered probable nest predators in that area.

The incubation of greater sandhill cranes has been found to average 30 days under natural conditions, with a range of 28 to 32 days (Walkinshaw, 1981a). There is no evidence of significant variations in incubation among the various subspecies.

### *Hatching and Postbreeding Biology*

Typically, a single day separates the time of hatching of the young in two-egg clutches. Newly hatched young are usually fed the eggshells from which they have hatched by the parent attending the nest, who breaks it up into very small pieces and feeds it to the young bill-to-bill. However, very little if any food is usually fed them on the first day. Yet, by the time they are about six hours old they often leave the nest a short distance, sometimes even swimming short distances. By the day after hatching the young are eating small items, and if the two eggs hatch on separate days the older chick often follows one of its parents away from the nest while the second one is being brooded. After both chicks are fairly strong they are generally taken away from the nest site by their parents, often into dry fields or drier marshy areas where insect foods are abundant (Walkinshaw, 1973).

TABLE 35  
Sources of Nesting Losses in Greater Sandhill Cranes

	<i>Idaho</i> <sup>1</sup>	<i>Oregon</i> <sup>2</sup>	<i>Michigan</i> <sup>3</sup>	<i>Michigan</i> <sup>4</sup>
Total Failed Nests	71	255	45	31
Lost to:				
Predation:	47.9%	92.1%	31.1%	7%
Desertion	8.5%	7.1%	24.4%	10%
Eggs addled or infertile	18.3%	.4%	31.1%	72%
Flooding or weather loss	2.8%	.4%	6.7%	—
Unknown causes	22.5%	—	4.4%	11%

<sup>1</sup>Drewien, 1973.

<sup>2</sup>Littlefield, 1976.

<sup>3</sup>Walkinshaw, 1981a.

<sup>4</sup>Hoffman, 1979 (percentages are of egg losses rather than nest losses).

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Fledging in the greater sandhill crane occurs at about three months of age. The exact time of fledging in lesser sandhill cranes is still unreported, but it is evidently longer than 60 days (Boise, 1976, 1977). In general, there is a relationship between the rate of development of young and the geographical distribution of the races, at least under captive rearing conditions (Baldwin, 1977a, b).

The rate of survival of young birds until autumn is probably fairly high in most cases. Walkinshaw (1981a) reported that 284 birds fledged out of 294 hatched young among Lower Peninsula nests, again suggesting a very high (96.5 percent) fledging rate. By comparison, Boise (1977) reported that 57 percent of the lesser sandhill crane chicks she observed in 1975 survived to fledging, while in 1976 the figure was 71 percent.

### RECRUITMENT RATES, POPULATION STATUS, AND CONSERVATION

Based on studies from 1952 to 1973, Walkinshaw (1981a) noted that during late summer the greater sandhill crane population in Michigan consisted of about 55 percent adult breeders, 16.6 percent fledged young, and 51 percent nonbreeders. This would mean that, on average, each breeding pair raised an average of 0.6 young to fledging during those years. This is a considerably smaller productivity rate than is indicated by hatching and rearing success rates estimated by him for the same area, suggesting that these rates are probably not representative for the Michigan crane population as a whole. Instead, a collective success rate of approximately 40 to 60 percent of the total eggs laid resulting in fledged young would seem to be typical of sandhill cranes, assuming that all of the paired birds lay two eggs, and that paired birds make up approximately half of the nonjuvenile population. This in turn would mean that the incidence of juveniles in the fall populations would be approximately 10 to 15 percent, or close to what seems to be fairly typical of sandhill cranes. Data summarized in table 8 indicate that the fall recruitment rates of sandhill cranes seem to range from about 8 percent to as high as 15.6 percent, averaging about 11 percent.

Walkinshaw (1981a) has attempted to provide a recent population estimate of the greater sandhill crane population, which he judged to be about 35,000. Of these, somewhat over half are associated with the West Coast and Rocky Mountain population, and about 11,000 are of the Great Lakes population.

The Canadian sandhill crane population perhaps numbers about 54,000 (Aldrich, 1979), although its

actual size is difficult to determine because of intergradation with the lesser sandhill crane. A more realistic estimate is one based on the total of the Pacific coast population of lesser sandhill cranes wintering in California (about 20,000 birds) plus the midcontinent population that winters primarily in Texas and New Mexico and stages in the Platte Valley. Estimates in the Platte Valley would suggest that this population is probably in the neighborhood of 250,000 birds. Assuming that no more than 50,000 of these are Canadian sandhills, then the total North American population of lesser sandhills might number about 200,000. This is considerably less than Johnson's population estimate of 250,000 to 400,000 lesser and Canadian sandhill cranes in the Central Flyway, on which he based his population modeling base. Clearly more reliable estimates of lesser and Canadian sandhill crane populations must be made before convincing judgments of the effects of present or possible future levels of sport hunting can be made.

The Florida sandhill crane is currently fully protected, and its population as of 1980 was approximately 5,000 birds. It has recently been receiving better protection, and is at least stable, although increased human population in southern Florida could eventually affect the crane population adversely (Walkinshaw, 1981a).

The Mississippi sandhill crane is at an extremely low population of about 40 to 50 birds, but also is essentially stable (Valentine, 1979, 1981). Valentine (1981) stated that the continued survival and increase of this population depend on an improvement of the habitat conditions within the existing refuge lands and an enlarged captive propagation and release program.

The status of the Cuban sandhill crane remains uncertain, but the most recent reports are that the birds on the mainland are now beginning to increase in numbers, or are at least stable. No information is available on the Isle of Pines population, which is probably the larger of the two components (Walkinshaw, 1981a).

### EVOLUTIONARY RELATIONSHIPS

Although obviously a part of the *Grus*, the sandhill has no strong behavioral similarities to other members of the genus (Archibald, 1975, 1976). Wood (1979) reported that morphologically the species seems to cluster in a loose group of *Grus* species that also includes the Eurasian crane, the hooded crane, and the white-naped crane, but no clear evidence for its nearest relatives emerged from his analysis.